A STUDY OF THE EFFECTS OF EXPATRIATION ON THE GONADS OF TWO MYCTOPHID FISHES IN THE NORTH ATLANTIC OCEAN

WILLIAM T. O'DAY[1] AND BASIL NAFPAKTITIS[1]

INTRODUCTION

Nearly a hundred years ago it was assumed that species of deep-sea fishes must have an unlimited horizontal distribution because of the apparent uniformity in their sunless environment. Material and knowledge have been increasing rapidly ever since, and we now know that even congeneric species can be localized in particular regions or water masses. We also know that some widely spread species can not reproduce away from their generally restricted spawning areas. Concerning this latter phenomenon, Ekman (1953: 317) wrote, "In some cases where a species occurs in a region as a dwarfed variety or with very few individuals, it may nevertheless reproduce itself to a sufficient extent and thus have its home there. But in other instances it remains questionable whether the species is able to exist independently in the unfavourable region or whether it would not die out there if it were not continuously reinforced from the more favourable regions." Ekman named the unfavourable region the expatriation area. His insight provided a new viewpoint for subsequent studies in zoogeography. "With the ever increasing store of specimens of bathypelagic fishes," wrote Ebeling (1962: 1), "along with accumulated data on their distributions and environment, it is now possible to discuss their zoogeography profitably; that is, to investigate not only what species are present and where they are, but also why they are there and how they got there."

Lantern fishes, family Myctophidae, offer good material for a study of expatriation in general and, especially, of its effects in the gonads at the cellular level. Most of them live at depths between 200 and 1,000 meters. Precise determination of the vertical distribution is complicated by several factors, especially the following: (1) distinct developmental stages are found at different depths; (2) after metamorphosis the fishes undergo extensive diurnal vertical migrations; (3) vertical distribution in the same species can vary in different areas.

Spawning depth seems to be species-specific. Fertilized eggs or newly hatched larvae float to the surface where they spend their larval life. Shortly before metamorphosis to the adult form, the pelagic larvae (probably due to changes in their specific gravity [Tåning, 1918: 19–20, 149]) sink to deeper layers where metamorphosis is completed. Then the newly metamorphosed fishes join the adults in their diurnal vertical migrations, and their life span may be as long as four or five years. Since they feed almost exclusively on zooplankton, their vertical migrations have been correlated with the similar movements of their prey. Many myctophids, as they approach sexual maturity, develop sexually dimorphic

[1] Department of Biological Sciences, University of Southern California, Los Angeles, California.

characters in the form of various luminous structures.

The present study is limited to the North Atlantic with particular respect to *Lobianchia dofleini* and *Lobianchia gemellari*, the distribution patterns of which have recently been worked out by Nafpaktitis (Dana Report, in preparation). The purpose of the study is to illustrate the effects of expatriation on the gonads at the cellular level.

We are greatly indebted to Dr. Ned Feder of the Biology Department, Harvard University, for his technical advice and for allowing us to use many facilities in his laboratory. We are especially grateful to Dr. Giles W. Mead of the Museum of Comparative Zoology, Harvard University, for his kindness in reviewing the manuscript and offering valuable advice and criticism. L. V. Worthington and R. H. Backus of the Woods Hole Oceanographic Institution have generously given of their time for profitable discussions concerning several ideas in this paper. Partial support was obtained through grant GF 147, from the National Science Foundation to Harvard University in support of oceanic ichthyology.

MATERIALS

A list of the specimens from which gonads were removed and sectioned for the present work (sizes are in standard length) is as follows:

Lobianchia dofleini

One female, 33 mm, BLUE DOLPHIN, sta. RHB 450, 39°45′N, 71°08′W, July 16, 1953, 75 fms; one female, 32 mm, BLUE DOLPHIN, sta. RHB 467, 39°37′N, 70°58′W, August 19, 1953, 24 fms; one female, 36 mm, BLUE DOLPHIN, sta. RHB 471, 39°48′N, 70°34′W, August 23, 1963, varied depths; one female, 34 mm, ATLANTIS, sta. RHB 459, 11°05′N, 63°40′W, July 25, 1963, 340 fms; one female, 37 mm, CAPTAIN BILL, sta. RHB 901, 38°52′N, 71°55′W, October 10, 1962, 300 fms; one female, 33.5 mm, CHAIN, cruise 17, sta. RHB 801, 00°15′S, 18°40′W, April 26, 1961, 85 m; two females, 46 mm and 26 mm, CHAIN, cruise 17, sta. RHB 803, 09°27′N, 27°15′W, May 1, 1961, 275 m; one female, 32.5 mm, ATLANTIS II, cruise 13, sta. RHB 1004, 11°29′N, 60°14′W, September 4, 1964, 330–395 m; one male, 33.6 mm, ATLANTIS II, cruise 13, sta. RHB 1005, 41°26.5′N, 59°01′W, September 4, 1964, 400–555 m; one female, 34.2 mm, ATLANTIS II, cruise 13, sta. RHB 1019, 41°53′N, 46°54′W, September 9, 1964, 400–410 m; one female, 34 mm, ATLANTIS II, cruise 13, sta. RHB 1041, 39°24′N, 27°11′W, September 21, 1964, 220–300 m; one female, 33 mm, GERONIMO, Bureau of Commercial Fisheries, Washington (BCFW) Cat. No. 324, 03°28′S, 00°14′W; one female, 27 mm, GERONIMO, BCFW Cat. No. 372, 31°49′N, 55°19′W.

The above material is deposited at the Museum of Comparative Zoology, Harvard University.

One female, 36 mm, and one male, 32 mm, WALTHER HERWIG, sta. 103, 14°30′N, 55°19′W, March 24, 1964, 900 m wire out. Institut für Seefischerei, Hamburg.

One female, 33 mm, CARYN, haul 23, 32°05.5′N, 65°20′W, July 23, 1948, 1,500 m wire out; one female, 28 mm, CARYN, haul 56, 32°07′N, 64°37′W, August 25, 1948.

The CARYN material is deposited at the Field Museum of Natural History, Chicago.

DANA material, deposited at the Danish Marine Biological Institute, Charlottenlund, Denmark, is listed below.

One female, 27.5 mm, sta. 1119 I, 36°08′N, 00°30′W, September 23, 1921, 300 m wire out; one female, 36 mm, sta. 1131 I, 36°11′N, 02°12′W, October 2, 1921, 400 m wire out; one female, 27 mm, and one male, 27.5 mm, sta. 1134 II, 36°08′N, 04°30′W, October 3, 1921, 300 m wire out; two females, 28.5 and 31 mm, sta. 1135 IV, 36°04′N, 05°05′W, October 4, 1921, 250 m wire out; one female, 40 mm, sta. 4157 IV, 44°01′N, 09°13′W, June 16, 1930, 300 m wire out; one female, 36 mm, sta. 4192 II, 39°57′N, 24°59′W, June 19, 1931, 600 m wire out; one female, 33 mm, sta. 4195 III, 41°55′N, 32°22′W, June 22, 1931, 300 m wire out; one female, 37 mm, sta. 4203 III, 49°49′N, 30°22′W, June 30, 1931, 300 m wire out.

Lobianchia gemellari

One female, 99 mm, CAPTAIN BILL II, sta. 19, 39°51′N, 71°13′W, June 23, 1952, 175–180 fms; one female, 101 mm, ATLANTIS, sta. RHB 162, 41°53′N, 64°23′W, July 28, 1953, 855 fms; two males, 37 and 57 mm, CHAIN, cruise 17, sta. RHB 808, 18°00′N, 39°00′W, May 5–6, 1961, 290 m; one female, 39 mm, CHAIN, cruise 17, sta. RHB 810, 20°55′N, 43°15′W, May 7, 1961, 495 m; one male, 45 mm, ATLANTIS II, cruise 13, sta. RHB 1020, 42°05′N, 46°29′W, September 9, 1964, 350–425 m; one female, 93 mm, ATLANTIS II, cruise 13, sta. RHB 1023, 43°16′N, 45°03′W, September 10, 1964, 520–700 m; one female, 50 mm, ATLANTIS II, cruise 13, sta. RHB 1026, 44°38′N, 43°55′W, September 11, 1964, 440 m; one female, 44 mm, ATLANTIS II, cruise 13, sta.

RHB 1044, 39°37′N, 31°10′W, September 26, 1964, 200–475 m.

The above material is deposited at the Museum of Comparative Zoology, Harvard University.

One female, 78 mm, WALTHER HERWIG, sta. 107, 14°30′N, 20°42′W, March 25, 1964, 900 m wire out. Institut für Seefischerei, Hamburg.

DANA material, deposited at the Danish Marine Biological Institute, Charlottenlund, Denmark, is listed below.

One female, 42 mm, sta. 1186 VI, 17°58′N, 64° 41′W, December 1, 1921, 1,000 m wire out; one female, 44 mm, sta. 1281 I, 17°43′N, 64°56′W, April 1, 1922, 1,000 m wire out.

METHODS

I. Postfixation. Acrolein postfixation proved unnecessary. Postfixed tissues were indistinguishable in histological sections from non-postfixed tissue. The postfixation procedure was as follows: the specimen was transferred from 72% ethanol to a solution of 10% acrolein in 72% ethanol, left overnight at 0°C, and then transferred to 100% ethanol and left at 0°C about 6 hours or longer. The latter step was repeated and then the tissue was dehydrated.

II. Dehydration. The specimens were transferred successively to the following solvents and left in them at 0°C for the indicated time:

(1) methyl cellosolve (ethylene glycol monomethyl ether) or 100% ethanol, 8–24 hours;
(2) n-propanol, 8–24 hours.

III. Embedding. Ovaries were impossible to section well in paraplast, a synthetic paraffin. Slightly better results were obtained with ester wax 1960, a very hard embedding medium, and polyester wax, a very soft (m.p. 37°C) embedding medium, which may be hardened during sectioning by being bathed in dry ice vapor. Both ester wax and polyester wax are described elsewhere (Steedman, 1960; Sidman, Mottla, and Feder, 1961).

Far better results were obtained with glycol methacrylate, a liquid monomer that polymerizes into a hard plastic when heated (Rosenberg *et al.*, 1960; Ashley and Feder, 1966). The "monomer mixture" contained 95 ml purified glycol methacrylate, 5 ml polyethylene glycol 200, and 0.15 g of catalyst (2,2′-azobis [2-methyl] propionitrile). Since the tissues were seldom larger than a few millimeters in diameter, one cc or less of 100% monomer mixture was sufficient to infiltrate them over a period of about two days. Just before polymerization, the tissues were stained for a few hours in a concentrated solution of acid fuchsin or safranin in 100% monomer mixture so that they could be seen in the hardened plastic for sectioning. Sections were cut at a thickness of one micron on a Porter-Blum microtome. Sections were floated on a drop of water on a glass slide and allowed to dry on the slide.

IV. Staining. Wax sections were stained in hematoxylin and eosin. Plastic sections were stained with toluidine blue or acid fuchsin followed by toluidine blue (Ashley and Feder, 1966). This was done by placing a drop of a concentrated aqueous solution of the dye on the section, and rinsing it in distilled water after the proper staining time, which was about four minutes or less for acid fuchsin and five minutes for toluidine blue. Stained sections were allowed to dry. Then they were mounted with permount and coverslipped.

V. Photographs. These were taken with Kodachrome II color film or Panatomic-X black-and-white film.

Lobianchia dofleini (Zugmayer)

Lobianchia dofleini (Fig. 1) is a stout little fish attaining a maximum size of about 48 mm in standard length and reaching sexual maturity at about 30 mm. Like its North Atlantic congener *L. gemellari*, *L. dofleini* shows striking secondary sexual dimorphism in the form of a series of luminous scale-like structures, which are located on the dorsal aspect of the caudal peduncle in males and on the ventral in females (Fig. 2).

L. dofleini is widely distributed in the North Atlantic (Fig. 3). It spreads across

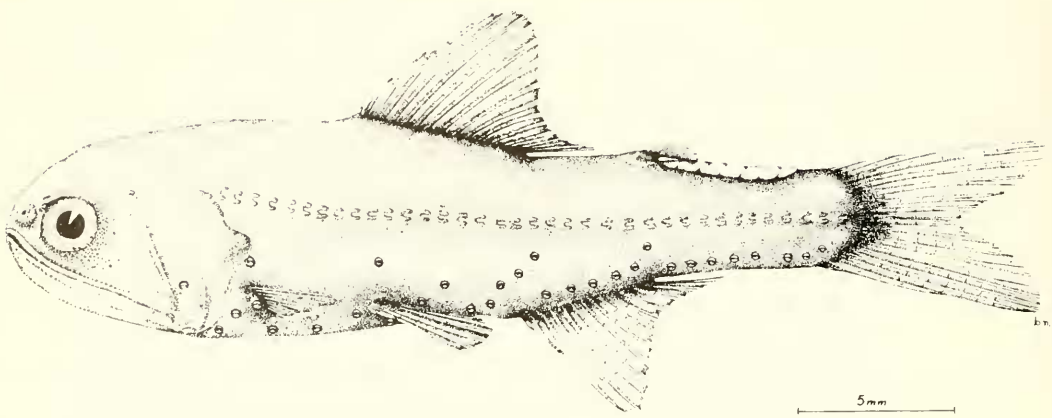

Figure 1. *Lobianchia dofleini* (Zugmayer, 1911). Male, 27 mm in standard length.

the ocean in a rather broad belt lying between the latitudes 26°N and 48°N. In spite of its wide distribution *L. dofleini* appears to have a reasonably well defined spawning range that includes the western Mediterranean Basin and the northeastern part of the North Atlantic, south of 48°N and east of 35° W.

This fish is not only widely distributed but is frequently taken in enormous numbers. With its wide distribution and abundance, its well developed swim bladder and its ability to undertake diurnal vertical migrations, it may well prove to be an important component of the deep scattering layers (D.S.L.), especially in the areas within its range where it is most numerous, i.e., off the coast of New England in the west, the western basin of the Mediterranean, and the adjacent waters of the North Atlantic in the east. Its properties as a sound scatterer have been discussed by Marshall (1951), and its probable involvement in the D.S.L. has been suggested by Hersey and Backus (1954).

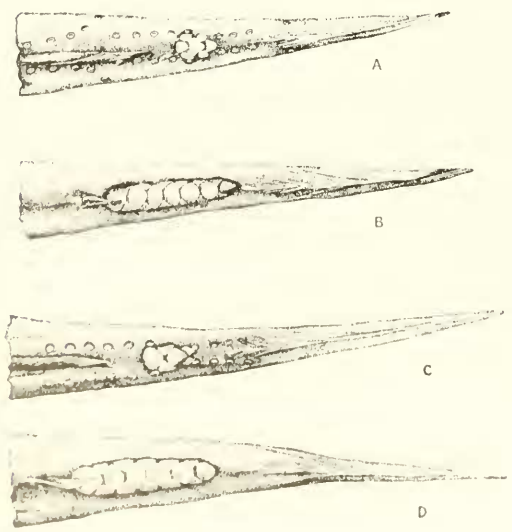

Figure 2. Luminous glands on caudal peduncle. *Lobianchia dofleini*: A, female; B, male. *L. gemellari*: C, female; D, male.

During the early stages of a systematic work on the species (Nafpaktitis, in preparation), it was noticed that females with ripe ova were becoming rare west of 30° W. This observation led to an extensive examination of many hundreds of specimens collected by various vessels in the western North Atlantic, west of 40° W, and north of 25° N. The results can be summarized as follows: (1) Not a single gravid female was found in collections made along and off the continental slope of the northeastern United States. At best, the gonads on gross examination appeared small and finely

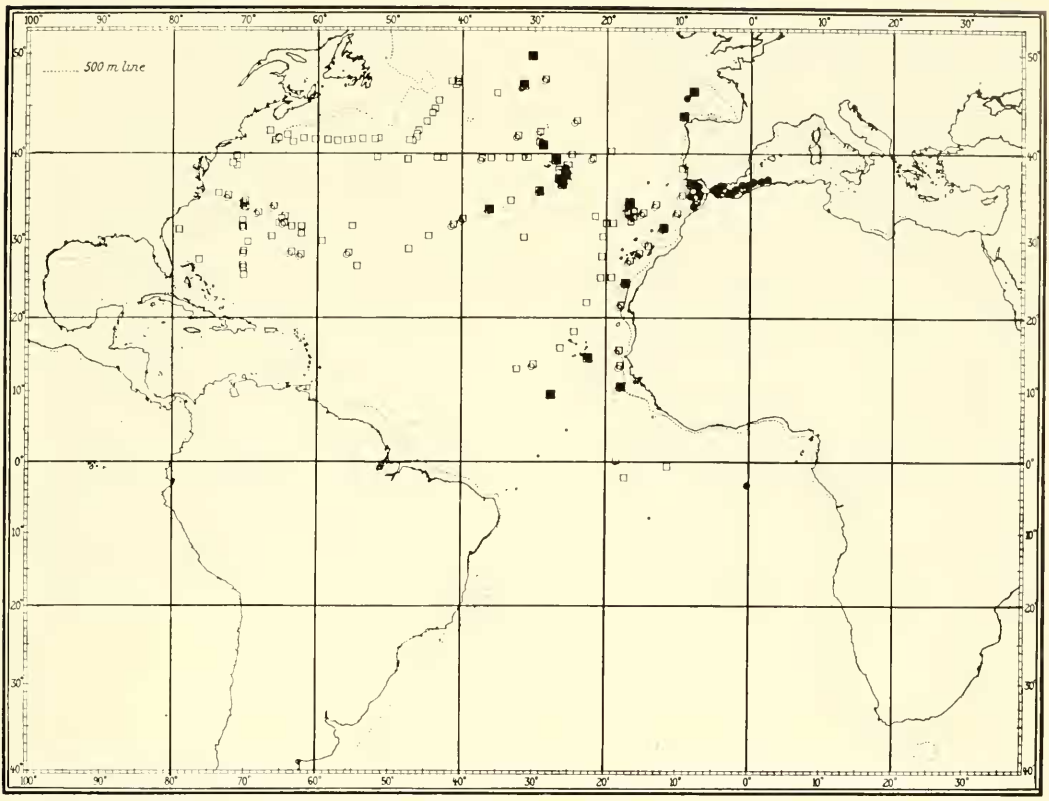

Figure 3. Distribution of *L. dofleini* in the North Atlantic. Solid dots represent gravid females; open squares, adults; solid squares, gravid females and adults; and circles, juveniles ≤ 12 mm in standard length.

granular, in spite of the fact that the caudal luminous structures in both sexes were fully developed. (2) In all collections along the continental slope and those north of 40°N, specimens smaller than 16 mm were absent. (3) Young stages, 11 mm to 12 mm, were found regularly along the R/V DANA transect from Cape Hatteras to Bermuda and from Bermuda to the Azores (Fig. 3).

The above findings aroused the suspicion that the population in the northwestern Atlantic consisted of expatriates which, under the hydrological conditions prevailing in that area, were incapable of reproducing. A histological examination of the gonads was subsequently undertaken.

Many specimens were sectioned, both from the expatriation area in the western North Atlantic and from the spawning grounds in the eastern North Atlantic, over a period of time extending throughout the summer and into early fall (see under *Materials*).

Results. The photomicrographs, Plate I, A and B, illustrate the differences between ovaries from specimens of *L. dofleini* taken in the reproductive area and those from specimens taken in the expatriation area. Expatriate specimens characteristically contained only oogonia and oocytes, while the relatively enormous yolk-filled eggs occurred only in ovaries of specimens from the spawning area. Expatriate oocytes contained no large yolk granules but did not appear abnormal. Their structure was entirely similar to that of a normal oocyte in

which vitellogenesis had not yet begun to a noticeable extent. Ovaries of females from the spawning area that are not preparing to spawn have many such oocytes.

Oocytes in early stages of development stain well with hematoxylin or toluidine blue. The developing oocyte grows greatly in size, the number of nucleoli increases, and a clear cytoplasmic zone separates the nucleus from a surrounding region of darker-staining cytoplasm, an effect which appears to be due to centrifugal migration of mitochondria and Golgi complexes (Droller and Roth, 1966). A faintly striated zona radiata, especially conspicuous in fish oocytes, can be seen in later stages of development. Eventually the oocyte is completely enclosed in a single layer of follicle epithelium and surrounded by thin connective tissue. Protein yolk stains well with acid fuchsin or eosin. The large, globular, non-staining cytoplasmic inclusions are apparently lipids (Chopra, 1960; Raven, 1961: 101–105; Droller and Roth, 1966).

Expatriate males had testes that contained mature sperm. The testis is composed of many lobules lined with germinal epithelium. Sperm are produced within these lobules and later move into a main duct. The entire structure is well vascularized and bound together by connective tissue (Hoar, 1957: 291). Mature sperm are small, hook-shaped cells that stain darkly with toluidine blue. Their delicate flagella are not preserved.

Discussion. Since the expatriate population is unable to reproduce itself, it must be maintained by regular transfusions of new individuals from the spawning area. The route over which these reinforcements arrive might be expected to follow the track of an ocean current, or series of currents, that integrate the expatriation area with the reproductive area. What is this route of constant reinforcement?

On the basis of hydrological evidence, L. V. Worthington of the Woods Hole Oceanographic Institution (Worthington, 1962) proposed a two-gyre system occupying the central and western North Atlantic (Fig. 4). The southern gyre, with Bermuda roughly in its center, extends to about 40° W. As it flows through the fringes of the spawning area, larvae and young stages are swept westward by it. Since the return flow of the southern gyre has an average velocity of about 10 cm per second (Worthington, personal communication), the young fishes could be transported from the fringes of the spawning area to the continental slope of North America in about one year. This time appears to be too long to account for the occurrence of 12 mm juveniles off Cape Hatteras, but little is known about fluctuations in the rate of transport and the duration of larval life. In view of present knowledge about the current system in the North Atlantic, the route proposed here seems to be the only feasible one. Under the influence of the westward flow, the expatriates will eventually reach the Gulf Stream. This current will rapidly carry them northward. Substantial numbers will enter the adjacent colder and less saline Slope Water (Iselin, 1936: 11) off the coast of the northeastern United States. Others

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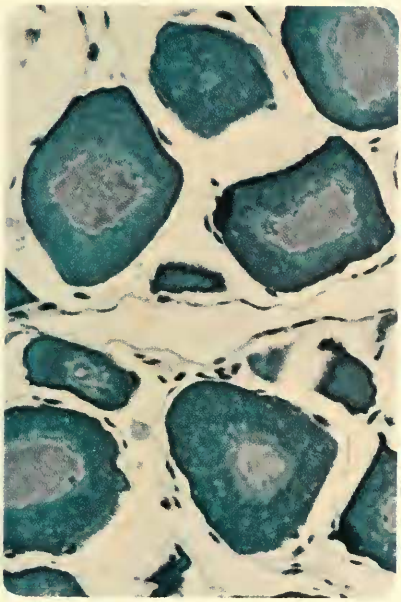
Plate I A Oocytes in the ovary of an expatriate *L. dofleini*, 34.2 mm in standard length; R V ATLANTIS II, cruise 13, sta. RHB 1019, 41 53'N, 46 54'W, September 9, 1964, 400–410 m depth. Glycol methacrylate, toluidine blue, × 400.

B: A single egg from the ovary of a specimen of *L. dofleini*, 31.0 mm in standard length, taken in the spawning area; R V DANA, sta. 1135 IV, 36 04'N, 05°05'W, October 4, 1921, 250 m wire out. Glycol methacrylate, acid fuchsin, toluidine blue, × 250.

C Partial view of cross section of testis of expatriate *L. gemellari*, 45.0 mm in standard length, showing cell divisions but no sperm, R V ATLANTIS II, cruise 13, sta. RHB 1020, 42°05'N, 46 29'W, September 9, 1964, 350–425 m depth. Glycol methacrylate toluidine blue, × 1,000.

D Partial view of testis of *L. gemellari*, 57.0 mm in standard length, taken in the spawning area. Hook-shaped cells are mature sperm. R V CHAIN, cruise 17, sta. RHB 808, 18°00'N, 39°00'W, May 5–6, 1961, 290 m depth. Glycol methacrylate, acid fuchsin, toluidine blue, × 1,000.



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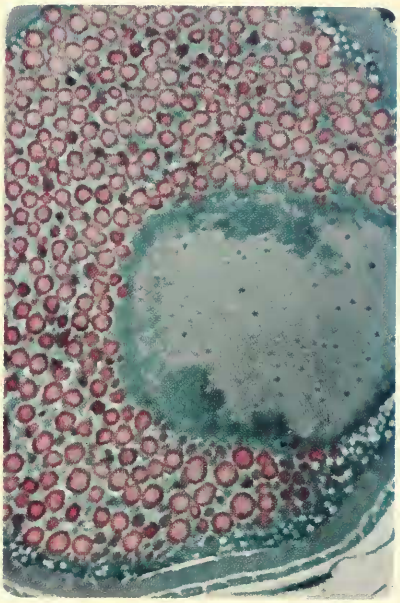

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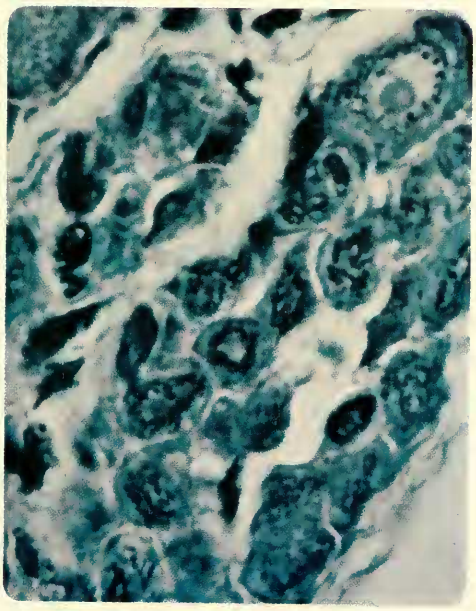

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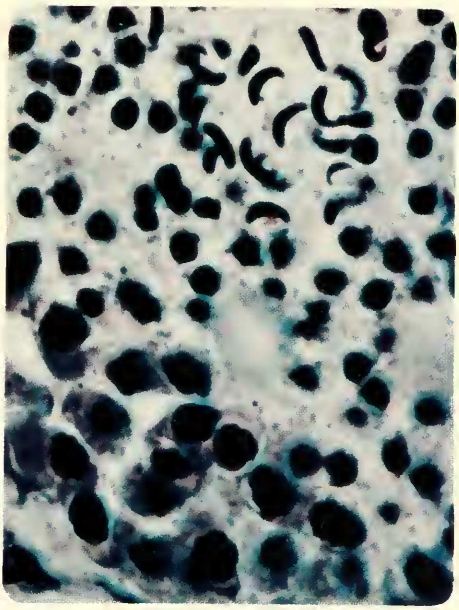

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Plate I

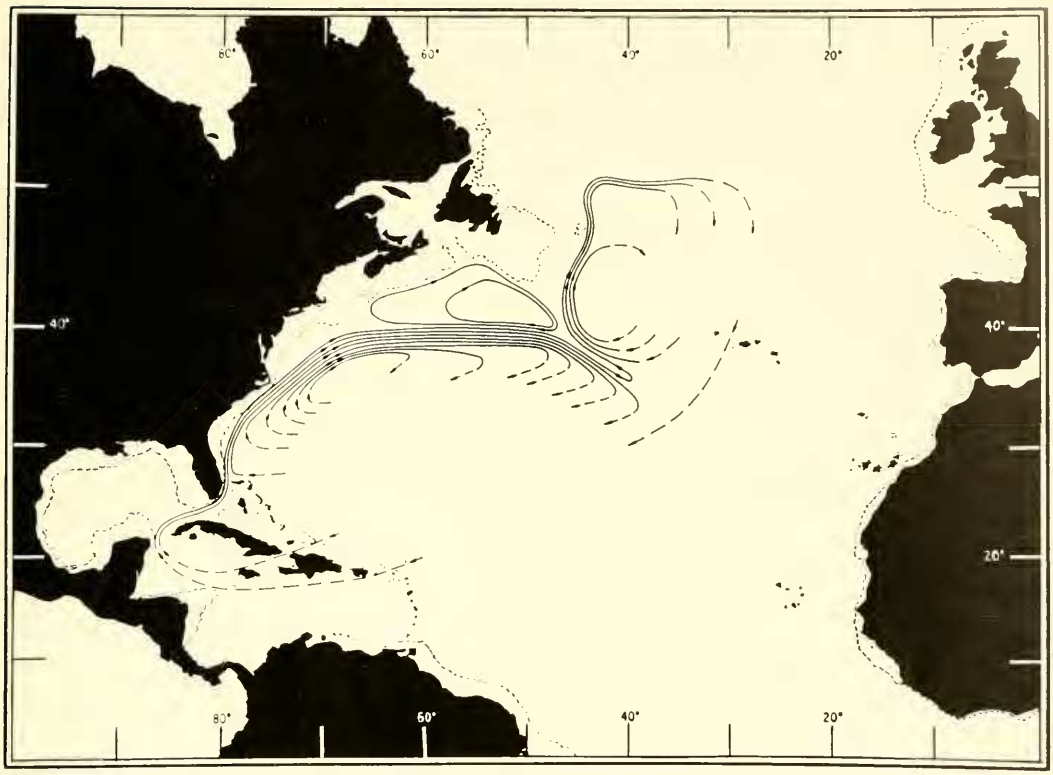

Figure 4. The two-gyre system proposed by Worthington (1962). Reproduced from Deep-Sea Research.

will remain in the Gulf Stream, while a few may follow the current until they return to the spawning grounds. In the expatriation area the young *dofleini*, apparently capable of adapting themselves to the physico-chemical factors, will grow to physical maturity. However, with ecological factors far from meeting the requirements of their reproductive physiology, these fishes will fail to reproduce.

There are remarkable differences between the temperature and salinity distributions in the expatriation area and the spawning area. Hjort (*in* Murray and Hjort, 1912: 444–445) wrote: "A peculiar feature is that all the [100 m] isotherms on the western side [of the North Atlantic] are quite close together, the water layers being squeezed between the oceanic subtropical waters from the south and the Labrador current from the north. All changes in temperature are therefore on the western side very sharp. On the eastern side the layers are spread out fan-wise, and as a consequence we may at a depth of 100 meters find the same temperature prevailing from north to south over wide areas . . ." The average temperatures at a depth of 200 m in the North Atlantic (Fig. 5) show a pattern very similar to that described by Hjort for the 100-meter isotherms. A temperature profile across the Atlantic at 40°N shows that there is a sharp convergence of isotherms above 2,000 m in a westward direction (Fig. 6). At the same latitude, the isohalines show a marked convergence from east to west (Fig. 7). Briefly, then, the variation in both temperature and salinity with depth is much

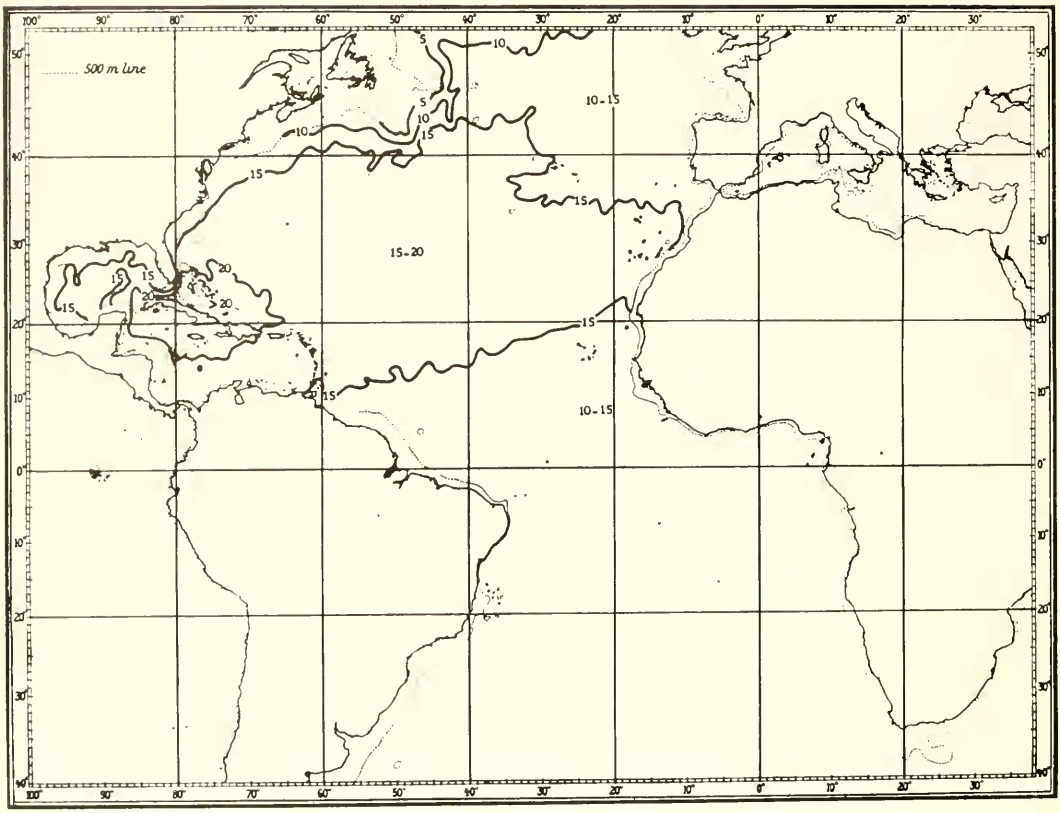

Figure 5. Average temperatures at a depth of 200 m in the North Atlantic. From Schraeder (1963, pl. 6).

greater in the expatriation area than in the spawning area. This variation is clearly reflected in the way the broadly spaced isotherms in the east converge, both horizontally and vertically, towards the northwestern North Atlantic.

The population of *Lobianchia dofleini* in the Slope Water off New England, which consists of adult individuals only, appears to be almost as dense as that in the spawning area. The Slope Water "is characterized by being the mixing zone, in the upper layers (down to 200 meters), for coastal water, which has escaped from over the

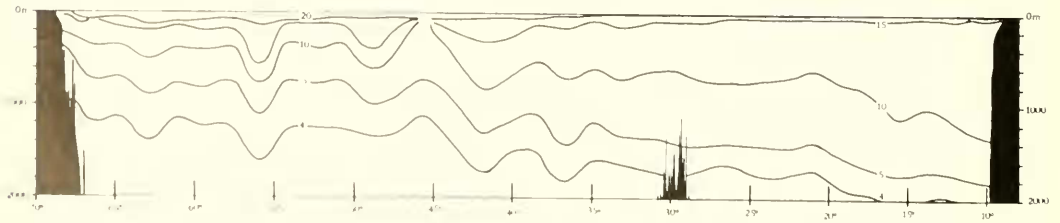

Figure 6. Temperature (°C) profile to a depth of 2,000 m at 40°N, from Georges Bank to Portugal (October 2–22, 1957). From Fuglister (1960: 41), intermediate isotherms omitted.

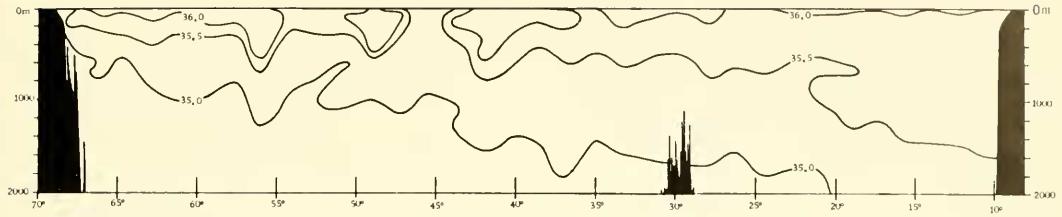

Figure 7. Salinity (‰) profile to a depth of 2,000 m at 40°N, from Georges Bank to Portugal (October 2–22, 1957). From Fuglister (1960: 79), intermediate isohalines omitted.

continental shelf, and Gulf Stream water, which has been carried west of the current's path" (Iselin, 1936: 11).

The broad stratification of both temperature and salinity in the water of the spawning area, and their much more narrow and less orderly distribution in the water of the expatriation area, suggest that stability of environment, within certain limits, may be a critical factor in the development of eggs.

Lobianchia gemellari (Cocco)

Expatriation from a subtropical environment to the same expatriation area inhabited by *L. dofleini* should produce similar or more severe effects in that expatriate. *L. gemellari* (Fig. 8), a species closely related to *L. dofleini*, confirms this expectation. Reaching sexual maturity at about 40 mm, *L. gemellari* is a somewhat larger fish than *L. dofleini*. It has a wide distribution, but is most abundant within a broad belt of warm water in the central North Atlantic (Fig. 9). Its spawning area includes the Caribbean Sea and adjacent waters.

Expatriation produces more drastic effects in *L. gemellari* than in *L. dofleini*. Not only are gametes of both sexes prevented from growing normally, but even secondary sexual characters fail to develop fully. Expatriate males are generally indistinguishable from expatriate females, although a few specimens show traces of sexually dimorphic luminous tissue on the

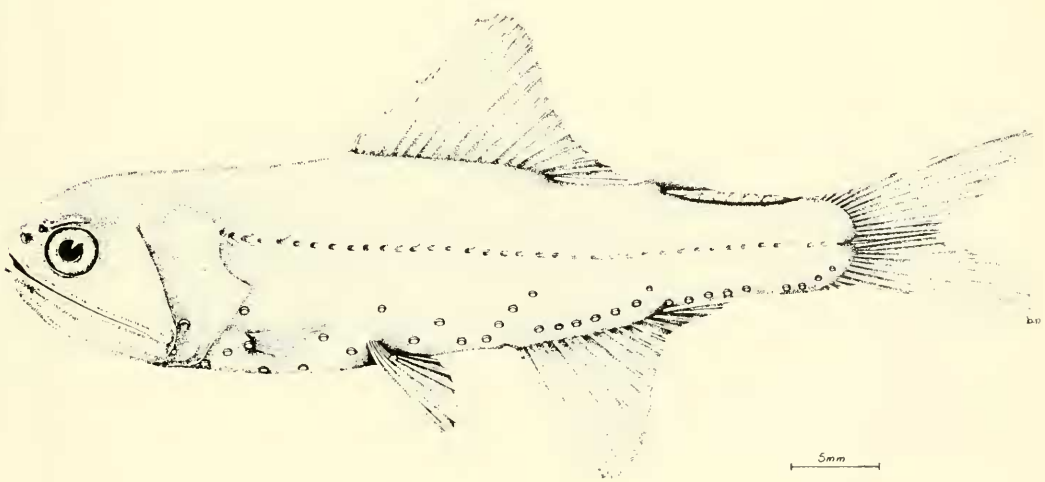

Figure 8. *Lobianchia gemellari* (Cocco, 1838). Male, 47.6 mm in standard length.

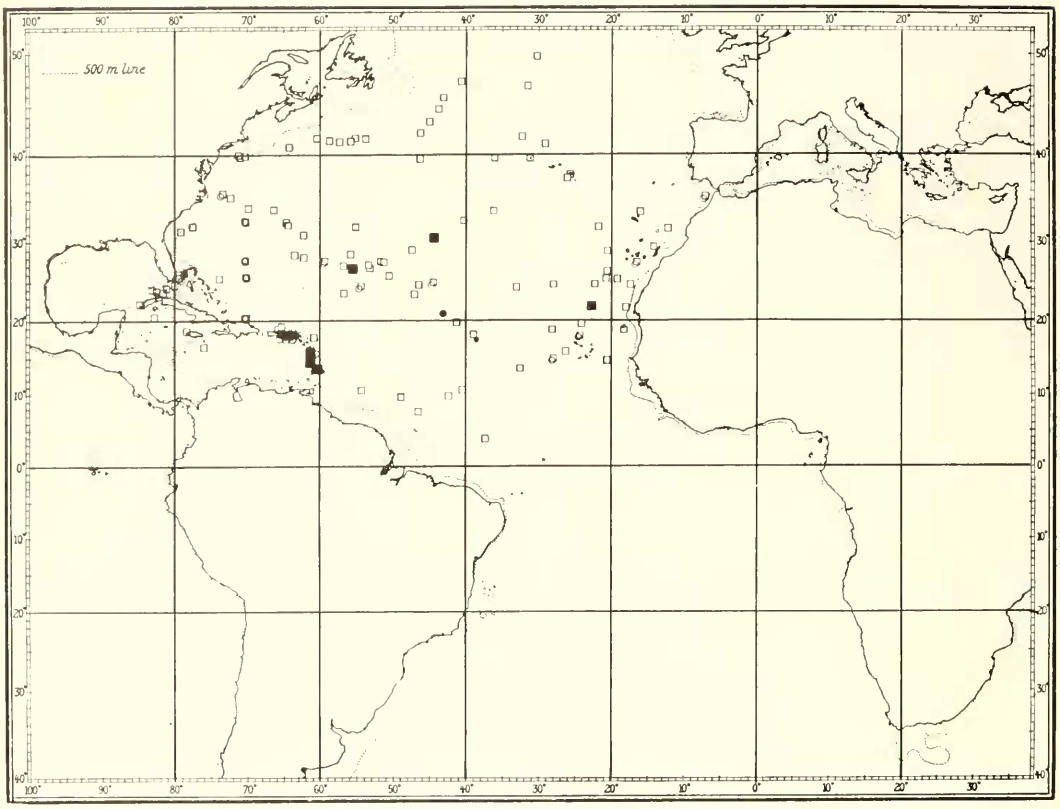

Figure 9. Distribution of *L. gemellari* in the North Atlantic. Solid dots represent gravid females; open squares, adults; solid squares, gravid females and adults; and circles, juveniles ≤ 12 mm in standard length.

caudal peduncle. Accordingly, histological examination was necessary to determine sex in most expatriate specimens of *L. gemellari*, for the gonads in both sexes were thread-like whitish structures. Ovaries in some specimens were evident from a barely visible granular consistency. In contrast, the ovaries of mature but non-spawning females of the reproductive area were far larger, yellow, and noticeably granular.

Results. Histological sections of ovaries from gravid females caught in the spawning area, show many large yolk-filled eggs and some growing oocytes (Plate II, A).

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Plate II. A. Several oocytes in different stages of development in the ovary of a specimen of *L. gemellari*, 42.0 mm in standard length, taken in the spawning area; R V DANA, sta. 1186 VI, 17° 58'N, 64° 41'W, December 1, 1921, 1,000 m wire out. Glycol methacrylate, acid fuchsin, toluidine blue, × 100.

B: Very small oocytes in the ovary of an expatriate *L. gemellari*, 50.0 mm in standard length; R V ATLANTIS II, cruise 13, sta. RHB 1026, 44 38'N, 43 55'W, September 11, 1964, 440 m depth. Glycol methacrylate, acid fuchsin, toluidine blue, × 1,000

C: Cross section through a lobule in the testis of a specimen of *L. dofleini*, 27.5 mm in standard length, from the spawning area; R V DANA, sta. 1134 II, 36 08'N, 04 30'W, October 3, 1921, 300 m wire out. Glycol methacrylate, toluidine blue, × 1,000.

D Cross section through a lobule in the testis of an expatriate *L. dofleini*, 33.6 mm in standard length; R V ATLANTIS II, cruise 13, sta RHB 1005, 41 26.5'N, 59 01'W, September 4, 1964, 400–555 m depth. Glycol methacrylate, toluidine blue, × 1 000

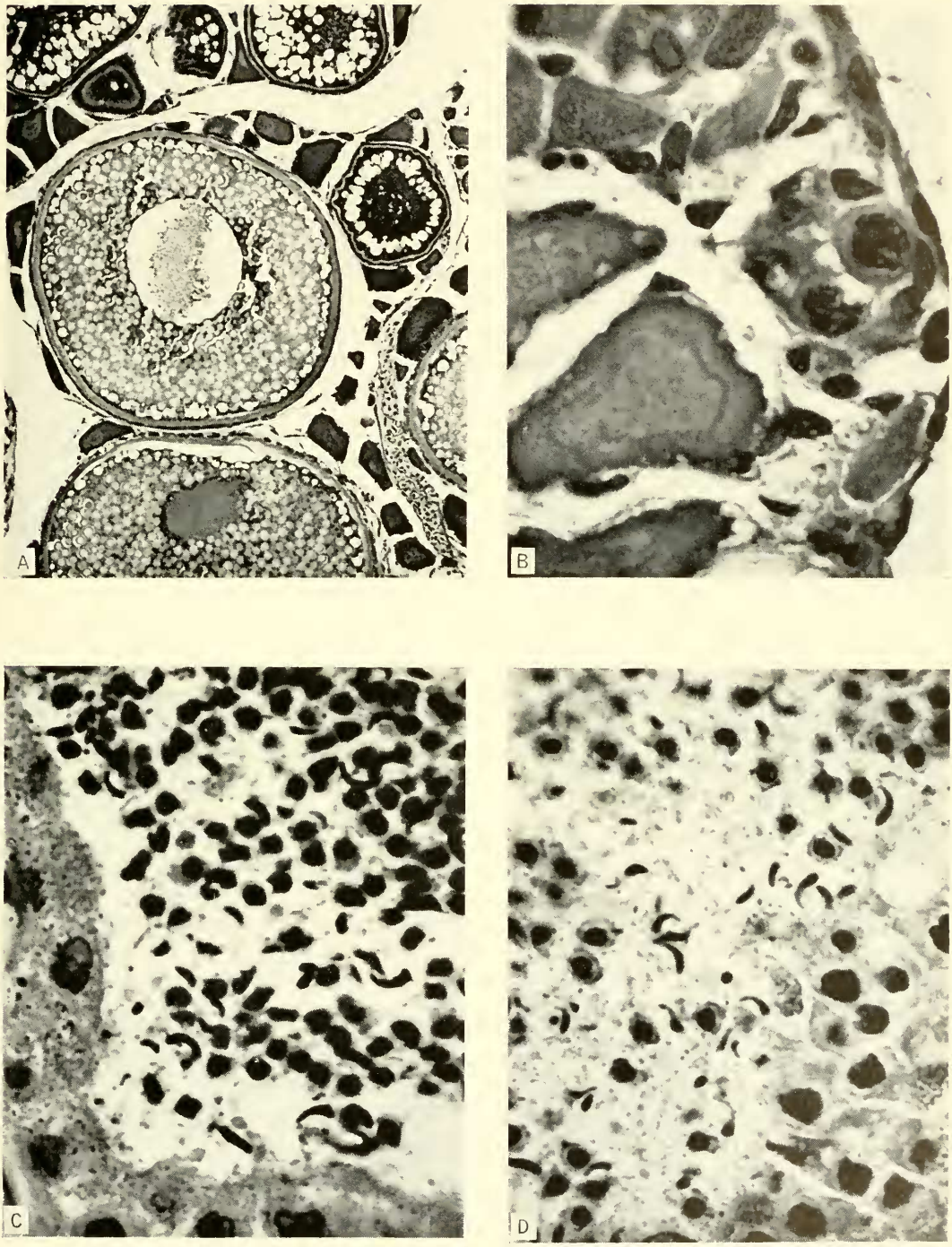

Plate II